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# Disruptions caused by invasive species and climate change on the functional diversity of a fish community

Allan T. Souza[1], Ester Dias[2], Carlos Antunes[2,3], Martina Ilarri[2]

**1** *Institute for Atmospheric and Earth System Research INAR, Forest Sciences, Faculty of Agriculture and Forestry, P.O. Box 27, University of Helsinki, 00014 Helsinki, Finland* **2** *Interdisciplinary Centre of Marine and Environmental Research (CIIMAR/CIMAR), University of Porto, Novo Edifício do Terminal de Cruzeiros do Porto de Leixões, Av. General Norton de Matos, s/n, 4450-208 Matosinhos, Portugal* **3** *Aquamuseu do Rio Minho, Parque do Castelinho, 4920-290 Vila Nova de Cerveira, Portugal*

Corresponding author: Allan T. Souza (allan.souza@helsinki.fi)

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## Abstract

As the effects of climate change continue to intensify, non-native species are becoming more prevalent in estuarine ecosystems. This has implications for the taxonomic and functional diversity of fish communities. Historically, biodiversity has been a synonym of taxonomic diversity, however this approach often fails to provide accurate insights on ecosystem functioning and resilience. To better understand how climate change is impacting fishes and their traits' composition, a long-term dataset from Minho Estuary (NW Iberian Peninsula) fish assemblage was analyzed. The results suggest that climate change and extreme weather events altered the prevailing trait modalities of fishes, which led to the overall decrease in functional diversity of the fish assemblage over the course of a decade. This decrease is associated to the loss of some trait modalities that are exclusively found in native species. On the other hand, the invasive species added novel traits associated with the conditions of high temperatures and low precipitation regime currently observed in the studied area. Our results highlight that the shift in the presence and dominance of some traits is directly influenced by climatic changes. Also, despite the addition of novel modalities by the invasive species, the fish assemblage is now less functional and taxonomically diverse than previously.

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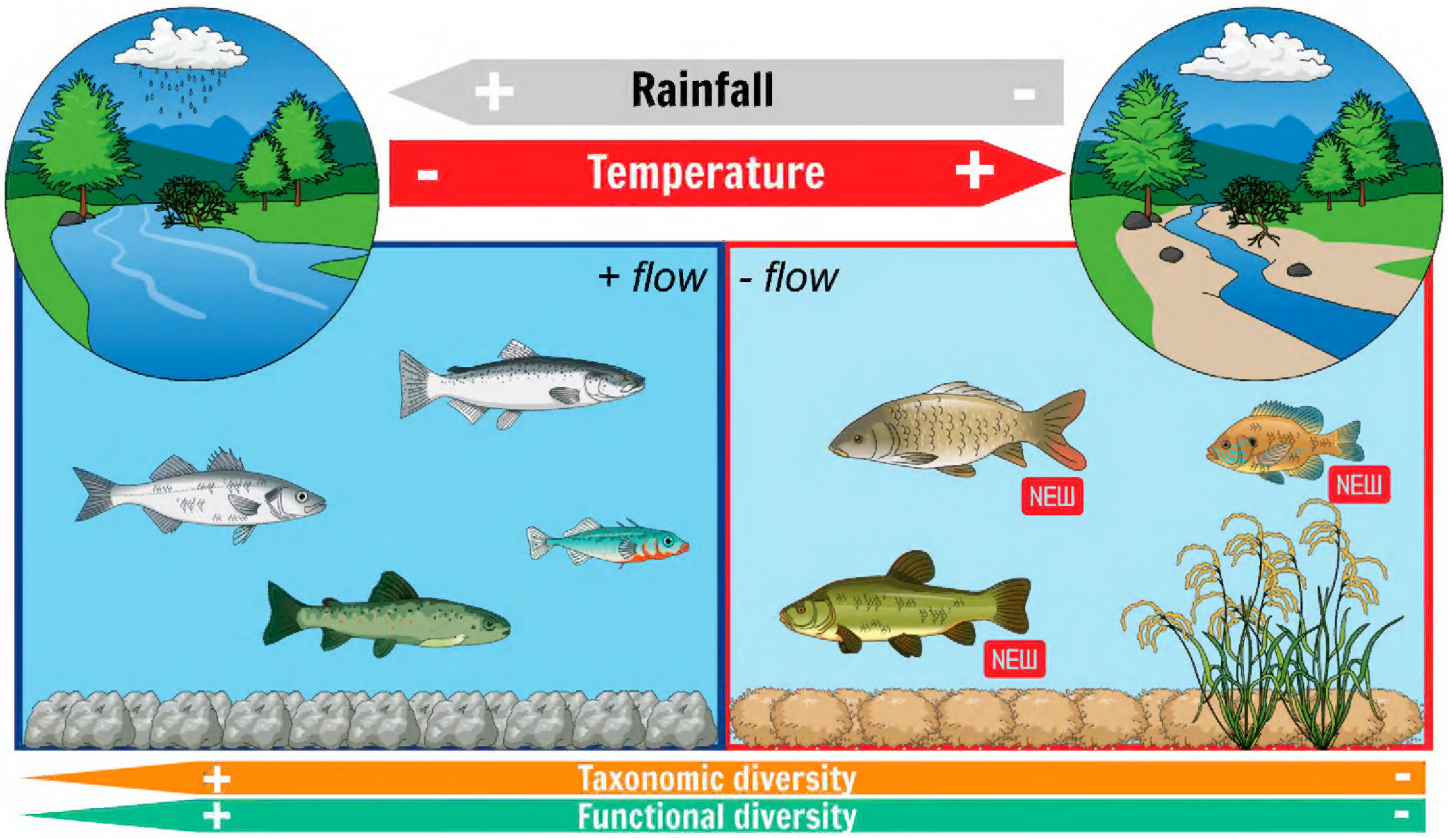
## Graphical abstract




**Keywords**

biodiversity, biological invasions, climatic events, ecosystem functioning, native species, traits

## Introduction

Climate change is one of the biggest threats to biodiversity currently (IPBES 2019; Reid et al. 2019), and nowadays many taxonomic groups and ecosystems around the world have already been affected (Alan Pounds et al. 2006; Moritz et al. 2008; Jarić et al. 2019). As global temperatures rise and weather patterns shift, ecosystems across the globe are undergoing drastic changes in their stability and functioning (Markham 1996; Walther et al. 2002; Parmesan and Yohe 2003). This can have a significant impact on the functional diversity of an ecosystem, as climate change can either favor certain species or cause the local extinction of others (Thuiller et al. 2006). The effects of climate change on functional diversity vary depending on the types of species present in a particular ecosystem. For example, species that are heat-tolerant may spread and flourish during periods of warmer climate; this is expected, for example, for the largemouth bass (*Micropterus salmoides*) in Iberian Peninsula (Bae et al. 2018). Other species, however, may be negatively impacted by shifts in temperature, which may translate into changes in species physiology, phenology, behavior, and geographic range (Robinson et al. 2009; Sorte et al. 2010; Hauser et al. 2018; Howard et al. 2020); this is the case for several tropical and subtropical fish species that have reach the northern Gulf of Mexico (Fodrie et al. 2010). Additionally, some species may require certain

conditions for foraging or nesting, and climate change may limit their access to these resources, thus preventing them from obtaining enough food and reproducing normally (Segev et al. 2014; Descamps et al. 2017). These factors collectively contribute to changes in functional diversity within ecosystems, leading to disruptions in populations and communities that vary depending on the compatibility between a species' ecological traits and the prevailing climatic conditions.

Historically, biodiversity has been associated to taxonomic diversity (Cardoso et al. 2014). However, this approach many times failed to provide insights into ecosystem functioning. Therefore, the use of traits and functional diversity indices alongside with taxonomic diversity provide a more holistic understanding about biodiversity (Hulme and Bernard-Verdier 2018). Both types of diversity metrics are important when evaluating the biodiversity of a given ecosystem (Villéger et al. 2010; Moore 2013; Teittinen and Virta 2021). In fact, due to the importance of functional diversity to biodiversity assessments, the number of scientific manuscripts integrating functional diversity into the ecological assessments has been increasing exponentially in recent years (Palacio et al. 2022). In general, ecosystems with high levels of both taxonomic and functional diversity are more stable and resilient to disturbances than ecosystems with low levels of diversity (Walker et al. 1999; Cadotte et al. 2011). By looking at the range of functions that different species perform in the ecosystem, the functional diversity indices provide a more in depth assessment of the ecosystem's overall condition. This is because a greater variety of functions creates greater redundancy within the system, meaning that if one species is lost, there are others that can perform its role in the ecosystem (Biggs et al. 2020).

On the other hand, climate change plays an important role in the establishment and spread of invasive species, a phenomenon that is widely recognized (Stachowicz et al. 2002). Currently, biological invasions are one of the most important topics in ecology (Anderson et al. 2021). The impacts of biological invasions can be extensive and often detrimental to native ecosystems (Pyšek et al. 2020). Invasive species can disrupt food webs (Wainright et al. 2021), alter habitats (Crooks 2002; Guy-Haim et al. 2018), displace native species (Catford et al. 2018), cause biodiversity loss (Pyšek et al. 2020), alter ecosystem functioning (Haubrock et al. 2021), and lead to significant social and economic impacts (Simberloff et al. 2013; Diagne et al. 2020). Invasive species can also out-compete native species for resources (Catford et al. 2018; Ferreira-Rodríguez et al. 2018), leading to a decline in diversity (Mollot et al. 2017; Williams-Subiza and Epele 2021) that can affect the entire ecosystem and affect various taxonomic groups that are directly or indirectly linked to them (Crooks 2002; Guy-Haim et al. 2018; Goedknegt et al. 2020; Vivó-Pons et al. 2020). Additionally, climate change is likely to exacerbate the impacts of biological invasions (Rahel and Olden 2008; Diez et al. 2012; Bellard et al. 2013), as rising temperatures and changes in precipitation regimes create new opportunities for the establishment of non-native species in new areas (Stachowicz et al. 2002; McKnight et al. 2021; Souza et al. 2022b).

While it is well documented that biological invasions usually have a negative impact on taxonomic diversity (Pyšek et al. 2020; Ilarri et al. 2022), few studies have

addressed the effects of this phenomenon on functional diversity (but see Sîrbu et al. 2022; Renault et al. 2022). Invasive species can fill empty trait gaps in the invaded ecosystems or replace the ones occupied by native species (Loiola et al. 2018), thereby disrupting functional diversity in these ecosystems (Hatfield et al. 2022; Linares et al. 2022). While the decline in taxonomic diversity can be accompanied by the loss of certain traits, it is crucial to understand how the decline in taxonomic diversity translates into changes in functional diversity, particularly in the context of simultaneous biological invasions and climate change. Hence, it is imperative to monitor ecosystem function and functional diversity as a means to address the threats posed by biological invasions and climate change. Through a continuous tracking of these indices, ecologists can identify areas at risk of species or functional loss (Santini et al. 2017) and pinpoint regions where appropriate management or conservation efforts are required.

Among the species groups particularly vulnerable to climate change and biological invasions are estuarine fishes (Gillanders et al. 2011; Souza et al. 2018; Lauchlan and Nagelkerken 2020; Ilarri et al. 2022). Despite their adaptability to a broad range of environmental conditions, these animals still exhibit sensitivity to the abiotic changes (e.g. in salinity and temperature) (Passos et al. 2016; Souza et al. 2018). Estuarine assemblages, in fact, often exhibit significant spatial and temporal variability (Sheaves 2009; Nagelkerken et al. 2015), emphasizing the importance of long-term datasets to facilitate a comprehensive assessment of fish assemblage dynamics and the influence of environmental drivers on them. Long-term monitoring data may also contribute to advances in invasion biology. In fact, there are few studies on the temporal aspects of invasive species impacts, and most of these studies are of short duration (less than 1 year), making it difficult to develop effective invasive management strategies and implement effective conservation measures (Matsuzaki et al. 2011). In addition, the use of traits can be useful in understanding invasion patterns and predicting which native species are most likely to be vulnerable to invasive species (Matsuzaki et al. 2011).

In this way, a long-term fish assemblage monitoring was conducted in the Minho Estuary (northwestern Iberian Peninsula) from 2010 to 2019. A recent study found that the Minho Estuary fish assemblage has been impacted by climatic changes and extreme temperature (heatwaves and cold-spells) and precipitation (dry and wet) events, which resulted in a less taxonomically diverse fish community dominated by a few invasive species (Ilarri et al. 2022). However, the temporal changes in the species trait composition of the Minho Estuary fish assemblage are still not known. To address this knowledge gap, a decade's worth of data on fish trait composition and climate (temperature and precipitation) from Minho Estuary were compiled from weekly *in-situ* fish sampling and satellite data. We hypothesize that climate change and extreme weather events alter the trait and functional diversity of estuarine fish communities, with most indices of functional diversity (e.g. functional divergence, dispersion, richness, evenness and RAO's quadratic entropy) being expected to decrease, while the functional redundancy is expected to increase. This is due to the increased prevalence of invasive species, which might introduce different traits compared to those originally found in the fish community, but also contribute to the loss or decline of some traits in the fish community.

# Methods

## Study area

Sampling took place in Lenta Marina, a small, semi enclosed bay (660 m × 80 m), located 14.5 kilometers upstream in the Minho Estuary (41°57'18.7"N, 8°44'42.9"W) (Fig. 1). Among the estuaries of Portugal, the Minho Estuary has relatively low levels of pollution (Reis et al. 2009), being used as a reference site in toxicology studies (Moreira et al. 2006; Guimarães et al. 2012). The Minho Estuary has also a significant history of biological invasions (Sousa et al. 2008, 2013; Ilarri et al. 2014), nevertheless, the number of invasive species in this area is comparatively lower than in other areas of the Iberian Peninsula (Muñoz-Mas et al. 2021). The Minho Estuary is described as mesotidal, with an average depth of 2.6 meters and a maximum depth of 26 meters (Alves 1997). It is partially mixed, except during flood periods when it tends to exhibit salt wedge conditions (Sousa et al. 2005). During summer or drought events, marine water enters the Lenta Marina as rainfall and water flow decrease (Ferreira et al. 2003). However, despite the occurrence of marine water intrusion, the influence of salinity in the Lenta Marina is relatively small. Salinity values typically range between 0 and 2.0 psu, with higher values observed in the late summer months or during dry periods (Sousa et al. 2013).

## Fish data

Fish samples were collected from January 2010 to November 2019, even though the samples were generally collected on a weekly basis, the actual intervals between samples varied slightly (Souza et al. 2023). The fyke nets were placed in fixed locations near the entrance of the peninsula where the Lenta Marina is harbored (Fig. 1). Double entry

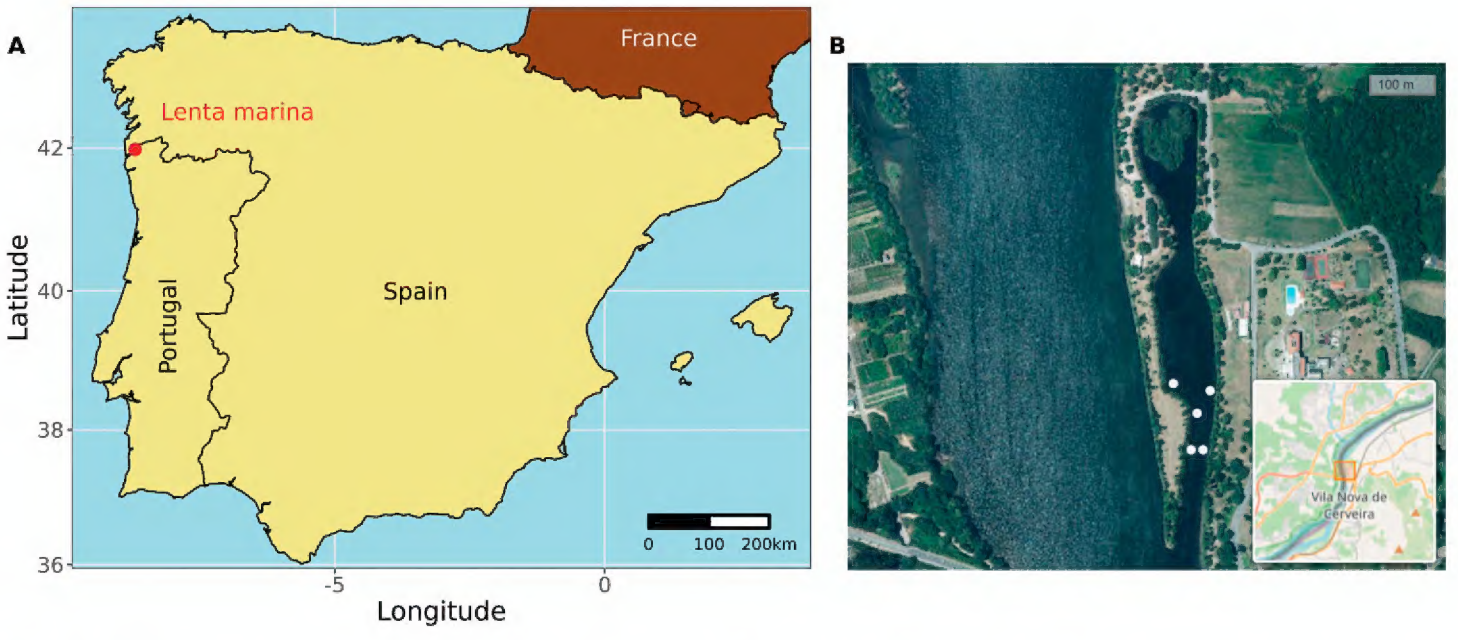



**Figure 1.** Representation of the study area (Lenta Marina) and sampling locations (Fyke nets) in the Minho estuary **A** map of the Iberian Peninsula showing the sampling site in the Minho estuary **B** an enlarged view of the study area highlighting the precise locations of the fyke nets (white circles) within the Lenta Marina.

fyke nets with a mesh size of 10 mm, measuring 7 meters in length, 0.7 meters in mouth diameter, and equipped with a 3.5 meter central wing, were used for the collection. These nets were always deployed in the morning and remained submerged for an average of 5.7 ± 3.5 days (mean ± SD). Once the fyke nets were retrieved, all captured fish were identified to the lowest taxonomic level and counted. In total, 3029 samples were collected throughout the study period. The average catch per unit effort (CPUE) per sampling date was determined by dividing the number of individuals caught by the number of days each fyke net remained in the water, taking into account the number of replicates per date. On average, 4.9 ± 0.4 fyke nets were used per sampling date, although this number varied due to technical limitations. A more detailed description of the sampling procedure can be found in a previous study by Ilarri et al. (2022).

## Trait composition

All fish species sampled in the Minho Estuary from January 2010 to November 2019 (more details in Ilarri et al. 2022) were analyzed according to 20 traits (14 biological and 6 ecological) containing 69 modalities (Appendix 1). The specific trait for each species and/or genera was classified following the information presented in the www.freshwaterecology.info database (see Appendix 2) (Schmidt-Kloiber and Hering 2015), that follows a single category assignment approach for fishes. When the value of any given species and trait was missing, the trait classification was complemented, if possible, with the information present in Cano-Barbacil et al. (2020). When the information of a particular trait modality was missing, NA (not available) was attributed to it, otherwise the values were either zeroes (0) or ones (1). The value used for each trait modality per sample was obtained by the computation of the community-weighted mean (CWM) using the function *dbFD* from the *FD* package in R (Laliberté et al. 2022). The CWM uses the classification of each species into a trait category as previously described and the abundance of species (in our case, CPUE) to compute the values of each modality per sample, which were used for further statistical analysis. In this study, we have compiled the trait composition data from 23 taxa (17 native and 6 non-native) (Table 1).

## Functional diversity indices

Six different functional diversity indices that were often used in previous studies (Villéger et al. 2008, van der Linden et al. 2016) to investigate the effects of environmental disturbances were selected. Functional diversity indices were calculated using the information on fish abundances and their traits classification, namely the functional divergence index (FDiv), the functional dispersion index (FDis), the functional richness index (FRic), the functional evenness index (FEve) (Villéger et al. 2008), Rao's quadratic entropy index (FRAO) (Lepš et al. 2006), and the functional redundancy index (FRed) (de Bello et al. 2007). The first five indices (FDiv, FDis, FRic, FEve and FRAO) were computed using the *dbFD* function from the *FD* package in R (Laliberté et al. 2022), while FRed was interpreted as a normed version of the mean functional similarity (Ricotta et al. 2016). The taxonomic index of diversity (Shannon's diversity

**Table 1.** Origin, family, species, vernacular name, total number of individuals captured (N), first record in the study area (only for the invasive species), and native range (only for the invasive species) of the fishes sampled from January 2010 to November 2019 in the Minho Estuary (Portugal). Fish species are ordered by origin and phylogenetic order (family).

| Origin | Family | Species | Vernacular name | N | 1st record | Native range |
|---|---|---|---|---|---|---|
| Native | Petromyzontidae | *Petromyzon marinus* | Sea lamprey | 12 | – | |
| Native | Anguillidae | *Anguilla anguilla* | European eel | 2971 | – | |
| Native | Clupeidae | *Alosa* spp. | Allis and twaite shads | 1 | – | |
| Native | Cobitidae | *Cobitis paludica* | Iberian loach | 9031 | – | |
| Native | Leuciscidae | *Achondrostoma arcasii* | Panjorca | 413 | – | |
| Native | Leuciscidae | *Pseudochondrostoma duriense* | Douro nase | 684 | – | |
| Native | Leuciscidae | *Squalius carolitertii* | Iberian chub | 20 | – | |
| Native | Salmonidae | *Salmo trutta* subsp. *fario* | Brown trout | 162 | – | |
| Native | Salmonidae | *Salmo trutta* subsp. *trutta* | Sea trout | 259 | – | |
| Native | Atherinidae | *Atherina boyeri* | Sand smelt | 1079 | – | |
| Native | Mugilidae | *Chelon auratus* | Golden grey mullet | 51 | – | |
| Native | Mugilidae | *Chelon labrosus* | Thicklip grey mullet | 28 | – | |
| Native | Mugilidae | *Chelon ramada* | Thinlip mullet | 1581 | – | |
| Native | Mugilidae | *Mugil cephalus* | Flathead grey mullet | 167 | – | |
| Native | Gasterosteidae | *Gasterosteus aculeatus* | Three-spined stickleback | 1221 | – | |
| Native | Moronidae | *Dicentrarchus labrax* | European seabass | 100 | – | |
| Native | Pleuronectidae | *Platichthys flesus* | European flounder | 1207 | – | |
| Invasive | Centrarchidae | *Lepomis gibbosus* | Pumpkinseed | 47302 | 2000s (Sousa et al. 2008) | ENA |
| Invasive | Centrarchidae | *Micropterus salmoides* | Largemouth bass | 570 | 1950s (Antunes 1990) | ENA |
| Invasive | Tincidae | *Tinca tinca* | Tench | 577 | 1990s (Antunes and Rodrigues 2004) | EUR |
| Invasive | Gobionidae | *Gobio lozanoi* | Iberian gudgeon | 255 | 1990s (Hervella and Caballero 1999) | IBE |
| Invasive | Cyprinidae | *Carassius auratus* | Goldfish | 20 | 1950s (Antunes 1990) | ASIA |
| Invasive | Cyprinidae | *Cyprinus carpio* | Common carp | 3146 | 1990s (Antunes and Rodrigues 2004) | ASIA, EU |

ENA = Eastern North America; EUR = Europe; IBE = Iberian Peninsula; ASIA = Eastern Asia

index) was calculated using the function diversity from the vegan package in R (Oksanen et al. 2022).

FDiv refers to how trait categories are distributed among individuals (Mason et al. 2005; Villéger et al. 2008). FDiv is low when the most abundant species have trait categories that are near the center of the trait space and high when the most abundant species have extreme trait categories (Mason et al. 2005). FDis measures the mean distance of the individual species from the center of the trait space occupied by the species, it computes the distance of the species from the mean dissimilarity (Villéger et al. 2008, van der Linden et al. 2016). FRic measures the amount of trait space filled by the species in the community. Typically, lower FRic values are associated with communities with similar traits (van der Linden et al. 2016; Maure et al. 2018). FEve measures the evenness of the distribution of the traits' abundance. It is the highest when there is an even distribution of species and abundance of traits (van der Linden et al. 2016). FRAO is an index that measures the trait dissimilarities in the community (Botta-Dukát 2005) and it is conceptually similar to FDis (Laliberté and Legendre 2010). FRed defines the extent

to which a community is saturated with species that have similar traits, with higher values indicating that the community is functionally redundant, while low values indicate that the functional redundancy in the community is low (de Bello et al. 2007).

## Climate data

Climate data used in this study included daily mean air temperature (measured 2 meters above ground level) in °C and precipitation in $mm.m^{-2}$. These data were scaled down to 1×1° grids and covered the entire duration of the sampling campaign, which ranged from January 2010 to November 2019. Data for the sampled site were obtained from NASA via their application programming interface (API) available through the NASA Langley Research Center (LaRC) POWER Project website. The jsonlite package in R developed by Ooms et al. (2022) was used to process the data.

Two different categories were used for the identification of extreme temperature events: cold spells and heat waves. The daily averages of air temperature were used to detect and determine the duration and strengthen of these extreme weather events. For this purpose, the *detect_event* function from the *heatwaveR* package in R, introduced by Schlegel and Smit (2021), was used. To assign a specific category to each climate extreme event, the category function from the same package was used, following the methodology described by Hobday et al. (2018).

To analyze precipitation patterns, the standard precipitation index (SPI) was calculated. The SPI quantifies the number of standard deviations by which the observed cumulative precipitation deviates from the climatological mean, as described by McKee et al. (1993). The daily precipitation data were processed using the *spi* function from the *precintcon* package (Povoa and Nery 2016). Based on the SPI values, each date was assigned to one of three precipitation state groups: normal (SPI greater than -1 and less than 1), dry (SPI less than -1) or wet (SPI greater than 1).

## Data analysis

Generalized additive models (GAM) with Gaussian distributions were used to assess the effects of temperature, precipitation and time on the fish trait means and diversity indices. Prior to analysis, the temperature and precipitation data were scaled (i.e. standardized with a mean of zero and a standard deviation of one) using the *scale* function from the *base* package in R (R Core Team 2023). CPUE values, diversity indices and precipitation data were appropriately transformed when necessary. Square root or log(X + 1) transformations were applied using the *sqrt* and *log1p* functions from the *base* package in R (R Core Team 2023).

For the temperature and precipitation data, cubic regression splines were used to smooth the variables for each season (winter, spring, summer and autumn). This smoothing process was carried out using the function *s* from the package *mcgv* (Wood 2022). The decision to apply smoothing by season was made in view of the different temperature patterns and precipitation profiles observed in each season, which are better captured when the penalty is applied on a seasonal basis.

As the dataset was a time series, the models from GAM included an autocorrelation structure with a lag effect. The initial value for the autocorrelation parameter (rho) was determined by running a GAM model without the autocorrelation structure. The *start_value_rho* function from the *itsadug* package (van Rij et al. 2022) was used to calculate the initial value of rho. Autocorrelation and partial autocorrelation were evaluated using the *acf* and *pacf* functions from the *stats* package in R package (R Core Team 2023). The GAM models were run with the *bam* function from the *mgcv* package (Wood 2022). All data analyses were performed using the R software, version 4.3.1 (R Core Team 2023).

### Data availability statement

Data used in this study are available for validation and further investigation. The fish occurrences dataset is archived on Zenodo (doi: 10.5281/zenodo.8279744), and detailed trait classification information can be found in Appendix 2. Climate data were sourced from the NASA using an API and a copy of the raw data and its description can be found in Suppl. material 1.

## Results

### Fish assemblage trait composition all over the years

Of the 67 fish traits modalities observed, 65.7% have varied significantly over time (Table 2). Temperature had correlated more strongly with trait modalities than precipitation, 59.7% of the traits modalities responded significantly to temperature, while 23.9% responded significantly to precipitation (Table 2). In addition, temperature correlated to the traits' modalities mostly during winter (59.7%) and autumn (46.3%). Precipitation influenced the trait modalities in a similar pattern, with winter (23.9%) and autumn (16.4%) having greater correlations than summer (7.5%) and spring (0%) (Table 2). Of the 67 GAM models for each trait modality, 19 had a percentage of explanation higher than 50% (Table 2, Fig. 2).

### Traits' composition associated with the invasive and native species

There were some traits' modalities that were more frequently associated with the native species, such as Diadromous (Migration), Litophilic and Other (Reproduction habitat), Freshwater-brackish-marine (Salinity), >=39 (Body length), Sh3 (Shape factor) and Winter time (Spawn time) (Fig. 3). On the other hand, it was also observed that other traits modalities were more frequently associated with invasive species such as Potamodromous (Migration), Benthopelagic (Habitat), Phytophilic and Phyto-litophilic (Reproduction habitat), Freshwater and Freshwater-brackish (Salinity), >15 (Life span), Sh1 (Shape factor), Sw3 (Swimming factor), 3–4 (Female maturity), Summer time (Spawn time), <=7 (Incubation period), 55k–60k

**Table 2.** Results of GAM models made to evaluate the effects of temperature, precipitation, and time on the fish assemblage trait composition of the Minho Estuary (Portugal). Statistical significance at: $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$. Win = winter, Spr = spring, Sum = summer, and Aut = autumn. The description of all modalities and their units can be found in Appendix 1.

| Trait | Modality | Temperature | | | | Precipitation | | | | Time | % exp. | $r^2$ adj. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Win | Spr | Sum | Aut | Win | Spr | Sum | Aut | F | | |
| Migration | Nom (No migration) | 0.76 | 0.05 | 1.74 | 0.73 | 0.60 | 0.05 | 3.41** | 5.80*** | -4.39*** | 15 | 0.124 |
| | Oce (Oceanodromous) | 2.25 | 3.69* | 1.79 | 0.97 | 0.00 | 1.66 | 1.41 | 0.01 | -1.55 | 4.6 | 0.028 |
| | Pot (Potamodromous) | 3.57** | 0.42 | 1.63 | 2.59 | 1.79 | 0.00 | 0.03 | 4.06* | 10.64*** | 58.3 | 0.572 |
| | Dia (Diadromous) | 4.09** | 0.12 | 2.43 | 8.93** | 0.75 | 0.52 | 0.06 | 1.41 | -4.07*** | 28.7 | 0.27 |
| Habitat | Ben (Benthopelagic) | 6.97*** | 0.26 | 1.07 | 10.86*** | 0.38 | 0.62 | 0.13 | 0.43 | 1.64 | 22.6 | 0.211 |
| | Dem (Demersal) | 3.54* | 1.34 | 0.31 | 6.67** | 1.23 | 0.18 | 0.08 | 0.08 | -2.7** | 12.9 | 0.112 |
| | Pel (Pelagic) | 12.15*** | 1.54 | 1.06 | 4.20* | 6.10*** | 0.42 | 0.01 | 0.23 | 2.48* | 24.5 | 0.223 |
| Rheophily | Lim (Limnophilic) | 9.53** | 0.16 | 1.17 | 2.74* | 1.04 | 0.84 | 0.28 | 0.55 | 1.81 | 11.8 | 0.104 |
| | Eur (Eurytopic) | 4.42** | 0.17 | 1.37 | 6.18* | 1.64 | 0.82 | 0.23 | 0.64 | 0.06 | 12.1 | 0.097 |
| | Rhe (Rheophilic) | 0.50 | 0.28 | 1.52 | 0.63 | 0.05 | 0.00 | 0.18 | 0.26 | -6.95*** | 15.9 | 0.144 |
| Feeding habitat | Benthivorous | 3.21* | 3.68 | 0.40 | 1.34 | 1.73 | 0.71 | 0.83 | 1.37 | -10.93*** | 49.3 | 0.48 |
| | Water column | 3.01* | 4.39* | 0.26 | 1.24 | 1.39 | 0.61 | 0.80 | 1.26 | 10.81*** | 50.8 | 0.496 |
| Reproduction habitat | Phy (Phytophilic) | 3.23* | 0.44 | 0.95 | 4.63* | 13.99*** | 0.03 | 1.06 | 1.47 | -1.88 | 11.1 | 0.091 |
| | Lit (Litophilic) | 2.64 | 0.07 | 1.53 | 2.59 | 0.03 | 0.24 | 0.09 | 0.30 | -5.09*** | 14.5 | 0.13 |
| | Phy (Phyto-litophilic) | 2.23 | 2.62 | 0.61 | 5.18* | 1.10 | 0.00 | 0.91 | 0.69 | 12.31*** | 61.8 | 0.61 |
| | Psa (Psammophilic) | 0.27 | 0.07 | 1.33 | 1.12 | 0.02 | 1.18 | 0.05 | 0.29 | -4.64*** | 10.8 | 0.091 |
| | Oth (Other) | 1.72 | 1.53 | 2.68 | 5.03* | 2.42 | 0.13 | 0.21 | 0.12 | -4.81*** | 12.9 | 0.114 |
| Salinity | Fre (Freshwater) | 3.64* | 0.00 | 3.11 | 7.95** | 0.02 | 1.35 | 0.46 | 0.23 | 3.81*** | 23.8 | 0.222 |
| | Frb (Freshwater-brackish) | 0.32 | 0.59 | 0.06 | 0.63 | 3.44 | 0.08 | 1.39 | 3.62* | -1.53 | 2.4 | 0.004 |
| | Fbm (Freshwater-brackish-marine) | 9.01*** | 0.01 | 3.18* | 12.22** | 2.18* | 0.18 | 0.01 | 0.29 | -3.51*** | 29.9 | 0.28 |
| | Fma (Freshwater-marine) | 1.31 | 1.23 | 0.97 | 0.03 | 0.01 | 1.63 | 0.05 | 1.17 | -0.40 | 3.0 | 0.014 |
| | Brm (Brackish-marine) | 0.00 | 0.07 | 1.30 | 7.23*** | 2.04 | 0.00 | 0.00 | 3.81*** | -1.72 | 14.3 | 0.117 |
| Feeding diet | Car (Carnivorous) | 0.78 | 1.23 | 1.33 | 2.82 | 1.17 | 0.47 | 0.01 | 2.96* | -3.75*** | 10.4 | 0.088 |
| | Inv (Invertivorous) | 1.37 | 1.26 | 0.18 | 0.26 | 0.40 | 0.68 | 0.15 | 0.00 | 13.44*** | 58.5 | 0.577 |
| | Omn (Omnivorous) | 0.06 | 3.28 | 1.16 | 0.22 | 0.04 | 1.77 | 0.11 | 1.11 | -11.77*** | 51.5 | 0.506 |
| | Oth (Other) | 3.42** | 0.09 | 0.01 | 0.00 | 1.67 | 0.04 | 0.02 | 0.00 | -1.73 | 4.4 | 0.023 |
| Life span | <8 | 2.75* | 2.04 | 1.18 | 0.00 | 5.34* | 0.51 | 0.17 | 0.38 | -15.91*** | 66.7 | 0.658 |
| | 8–15 | 4.01** | 1.40 | 0.72 | 3.94* | 9.80** | 0.08 | 0.84 | 0.98 | 16.63*** | 70.5 | 0.699 |
| | >15 | 0.08 | 0.05 | 0.61 | 5.44* | 0.24 | 0.33 | 0.32 | 1.73 | -1.06 | 3.40 | 0.017 |
| Body length | <=20 | 3.37 | 0.13 | 0.05 | 1.59 | 0.84 | 1.42 | 0.49 | 0.99 | 2.74** | 10.6 | 0.09 |
| | 20–39 | 6.66*** | 0.96 | 1.74 | 0.90 | 2.20* | 1.45 | 3.84*** | 4.71* | -2.61** | 12.2 | 0.088 |
| | >=39 | 1.07 | 0.23 | 0.71 | 7.70** | 0.24 | 0.12 | 0.30 | 2.02 | -1.31 | 5.3 | 0.037 |
| Body shape | Sh1 (<= 4.35) | 4.21** | 0.63 | 2.44 | 7.19** | 0.94 | 0.03 | 0.77 | 1.03 | 11.29*** | 58.8 | 0.577 |
| | Sh2 (4.35–4.78) | 2.25 | 3.69* | 1.79 | 0.97 | 0.00 | 1.66 | 1.41 | 0.01 | -1.55 | 4.6 | 0.028 |
| | Sh3 (4.78–5.6) | 14.07*** | 2.32 | 4.61** | 4.38* | 3.32** | 1.40 | 0.09 | 0.28 | -3.34*** | 32.9 | 0.309 |
| | Sh4 (>=5.6) | 3.44* | 1.06 | 3.18 | 9.67** | 4.18* | 0.29 | 0.06 | 0.14 | -1.82 | 11.9 | 0.103 |

| Trait | Modality | Temperature | | | | Precipitation | | | | Time | % exp. | $r^2$ adj. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Win | Spr | Sum | Aut | Win | Spr | Sum | Aut | F | | |
| Swimming factor | Sw1 (Fast swimmer) | 0.20 | 4.06*** | 5.07** | 0.41 | 0.08 | 2.02 | 0.02 | 0.86 | -8.97*** | 30.0 | 0.283 |
| | Sw2 (Average swimmer) | 13.89*** | 0.96 | 3.71 | 8.69** | 0.94 | 0.15 | 0.15 | 0.86 | -0.26 | 26.6 | 0.251 |
| | Sw3 (Slow swimmer) | 9.05*** | 3.48* | 1.69 | 3.03 | 3.29 | 0.02 | 0.03 | 0.33 | 17.84*** | 69.7 | 0.69 |
| Female maturity | <=2 | 4.00** | 2.57 | 3.49* | 0.00 | 5.75* | 1.07 | 2.09* | 0.00 | -16.68*** | 66.5 | 0.655 |
| | 2–3 | 2.69* | 0.01 | 6.84*** | 0.80 | 0.27 | 0.13 | 7.01*** | 1.22 | -4.17*** | 19.0 | 0.162 |
| | 3–4 | 0.16 | 0.48 | 0.01 | 0.94 | 2.03 | 0.03 | 0.64 | 2.29 | -0.63 | 1.1 | -0.006 |
| | 4–5 | 4.12** | 1.37 | 0.00 | 1.53 | 9.21** | 0.15 | 0.62 | 2.34 | 14.62*** | 70.7 | 0.7 |
| | >=5 | 0.60 | 1.43 | 3.06 | 9.03** | 0.40 | 0.41 | 0.13 | 0.33 | -1.72 | 6.7 | 0.051 |
| Spawn time | Winter time | 3.23* | 3.61 | 0.35 | 2.16 | 2.85* | 1.56 | 0.01 | 0.71 | -10.24*** | 51.1 | 0.499 |
| | Summer time | 3.30** | 3.53 | 0.37 | 1.86 | 4.01* | 1.41 | 0.03 | 1.31 | 10.12*** | 53.8 | 0.528 |
| Incubation period | <=7 | 4.72*** | 3.41 | 1.54 | 5.37* | 2.26 | 0.94 | 0.18 | 0.68 | 10.04*** | 55.0 | 0.538 |
| | 7–14 | 3.42** | 0.09 | 0.01 | 0.00 | 1.67 | 0.04 | 0.02 | 0.00 | -1.73 | 4.4 | 0.023 |
| | >14 | 10.69*** | 1.68 | 2.01 | 1.87 | 5.35*** | 0.75 | 0.03 | 0.01 | 0.72 | 24.1 | 0.219 |
| Fecundity | <=55k | 2.70* | 1.98 | 1.35 | 0.01 | 4.57* | 0.52 | 0.27 | 0.36 | -16.74*** | 67.7 | 0.668 |
| | 55k-60k | 1.31 | 2.27 | 0.55 | 3.87 | 0.56 | 0.00 | 0.92 | 0.78 | 12.18*** | 60.3 | 0.595 |
| | >60k | 0.02 | 0.03 | 0.01 | 4.09* | 0.06 | 0.44 | 0.93 | 0.91 | -1.30 | 3.5 | 0.018 |
| Relative fecundity | >=57 | 0.44 | 0.03 | 1.32 | 0.20 | 0.13 | 0.02 | 1.82 | 4.80** | -4.71*** | 14.0 | 0.12 |
| | 57–200 | 0.14 | 0.90 | 0.27 | 0.38 | 1.83 | 0.06 | 1.43 | 3.67** | -0.99 | 1.6 | -0.008 |
| | >200 | 4.70*** | 0.72 | 4.85* | 4.68* | 4.29*** | 1.36 | 0.06 | 0.25 | -1.45 | 18.8 | 0.165 |
| Egg diameter | <1.35 | 7.35*** | 0.80 | 3.21 | 4.54* | 1.98 | 0.12 | 0.30 | 0.60 | 6.05*** | 29.5 | 0.282 |
| | 1.35–2 | 2.03 | 0.05 | 3.47 | 1.39 | 11.80*** | 0.15 | 0.50 | 2.79* | -6.98*** | 25.9 | 0.244 |
| | >2 | 6.37*** | 0.16 | 3.49 | 9.91** | 0.26 | 0.06 | 0.21 | 0.06 | -5.23*** | 21.4 | 0.199 |
| Larval length | <=4.2 | 9.93*** | 8.81** | 0.29 | 2.23 | 3.68 | 0.38 | 0.45 | 1.47 | 15.6*** | 64.3 | 0.636 |
| | 4.2–6.3 | 0.30 | 1.04 | 0.04 | 0.22 | 3.10 | 0.00 | 2.03 | 3.78** | -1.46 | 2.1 | 0.001 |
| | >6.3 | 6.31*** | 0.16 | 3.51 | 9.94** | 0.26 | 0.06 | 0.21 | 0.18 | -5.26*** | 21.5 | 0.199 |
| Parental care | Phn (Protection with nester or eggs hiders) | 3.44* | 4.61* | 0.20 | 4.44* | 1.92 | 0.99 | 0.98 | 0.60 | 10.65*** | 57.0 | 0.561 |
| | Nnh (No protection with nester or eggs riders) | 6.99*** | 0.13 | 3.88* | 10.26** | 0.26 | 0.08 | 0.18 | 0.06 | -5.42*** | 22.0 | 0.205 |
| | Nop (No protection) | 9.37** | 0.01 | 0.64 | 6.35* | 0.42 | 1.15 | 1.01 | 0.59 | -0.93 | 11.7 | 0.099 |
| Larval stage duration | <12 | 0.17 | 0.50 | 2.14 | 0.02 | 2.60 | 0.14 | 2.29* | 5.78*** | -2.09* | 6.1 | 0.032 |
| | 12–25 | 2.02 | 2.66 | 0.12 | 2.02 | 1.50 | 0.01 | 0.76 | 2.05 | 11.86*** | 63.0 | 0.62 |
| | >25 | 7.27*** | 0.28 | 1.25 | 5.37* | 0.78 | 0.06 | 0.31 | 0.02 | -5.31*** | 14.0 | 0.123 |

(Fecundidty), 57–200 (Relative fecundity), <1.35 and 1.35–2 (Egg diameter), <=4.2 and 4.2–6.3 (Larval length), Nop (No protection) (Parental care) and <12 (Larval stage duration) (Fig. 3).

## Extreme weather events

Over the study period, there were 52 extreme temperature events (19 heatwaves: 9 moderate and 10 strong; 33 cold-spells: 32 moderate and 1 strong), and 44 extreme

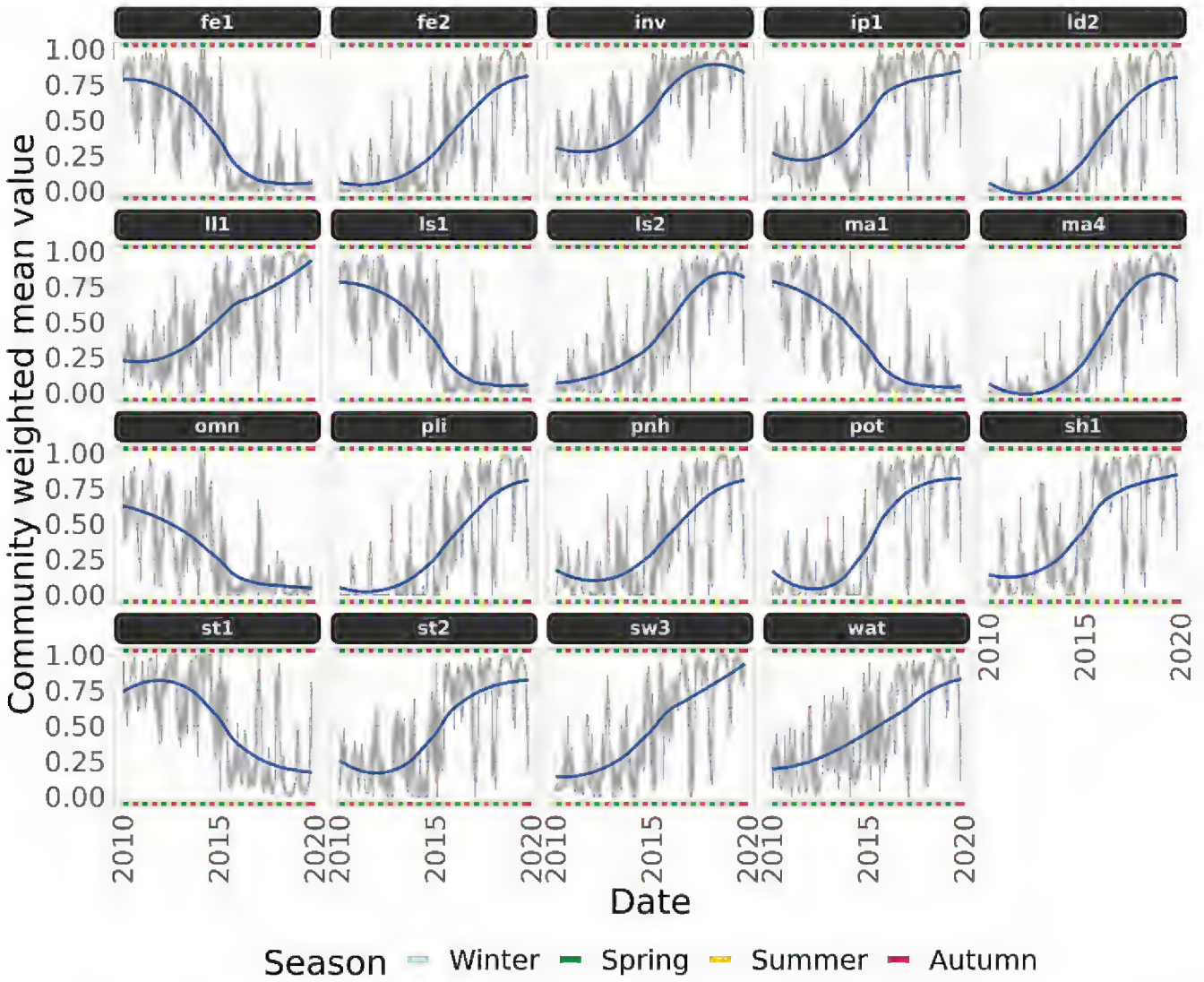



**Figure 2.** Selection of fish trait modalities in the Minho Estuary (Portugal) that had strong temporal changes (selected by the highest % of variation). Blue lines refer to a simple moving regression (loess) and are only indicative of the temporal changes. Statistical tests can be found in Table 2. fe1 = number of oocites less or equal to 55000, fe2 = number of oocites between 55000 and 60000, inv = invertivorous (feed on invertebrates), ip1 = incubation period is less or equal to seven days, ld2 = larval stage duration between 12 and 25 days, ll1 = larval length is smaller or equal to 4.2 cm, ls1 = life span is less than eight years, ls2 = life span is between eight and fifteen years, ma1 = females are mature before two years, ma4 = females are mature between four and five years, omn = omnivorous (feed on animals and plants), pli = reproduction habitat is phyto-litophilic (associated with plants and rocks), pnh = parental care by protection with nesting or egg hiding, pot = potamodromous migration (between different freshwater bodies), sh1 = shape factor ratio is smaller or equal to 4.35 (compact, rounded body shape), st1 = spawn time is during winter, st2 = spawn time is during summer, sw3 = slow swimmer, wat = feeding habitat is in the water column. The description of all modalities and their units can be found in Appendix 1.

precipitation events (21 dry and 23 wet) in the area of the Minho Estuary sampled. For more details see Ilarri et al. (2022).

The moderate heatwave events correlated positively and negatively with some trait modalities, and of these, only 1.5% of the traits had a strong decrease in their mean value during these kind of extreme events (e.g., Salinity: Brackish-marine, decrease of 100%), and about 4.5% had a strong increase (Migration: Oceanodromous, increase of 316%; Shape factor: 4.35–4.78, increase of 316%; Reproduction habitat: Psammophilic, increase of 117%) (Table 3).

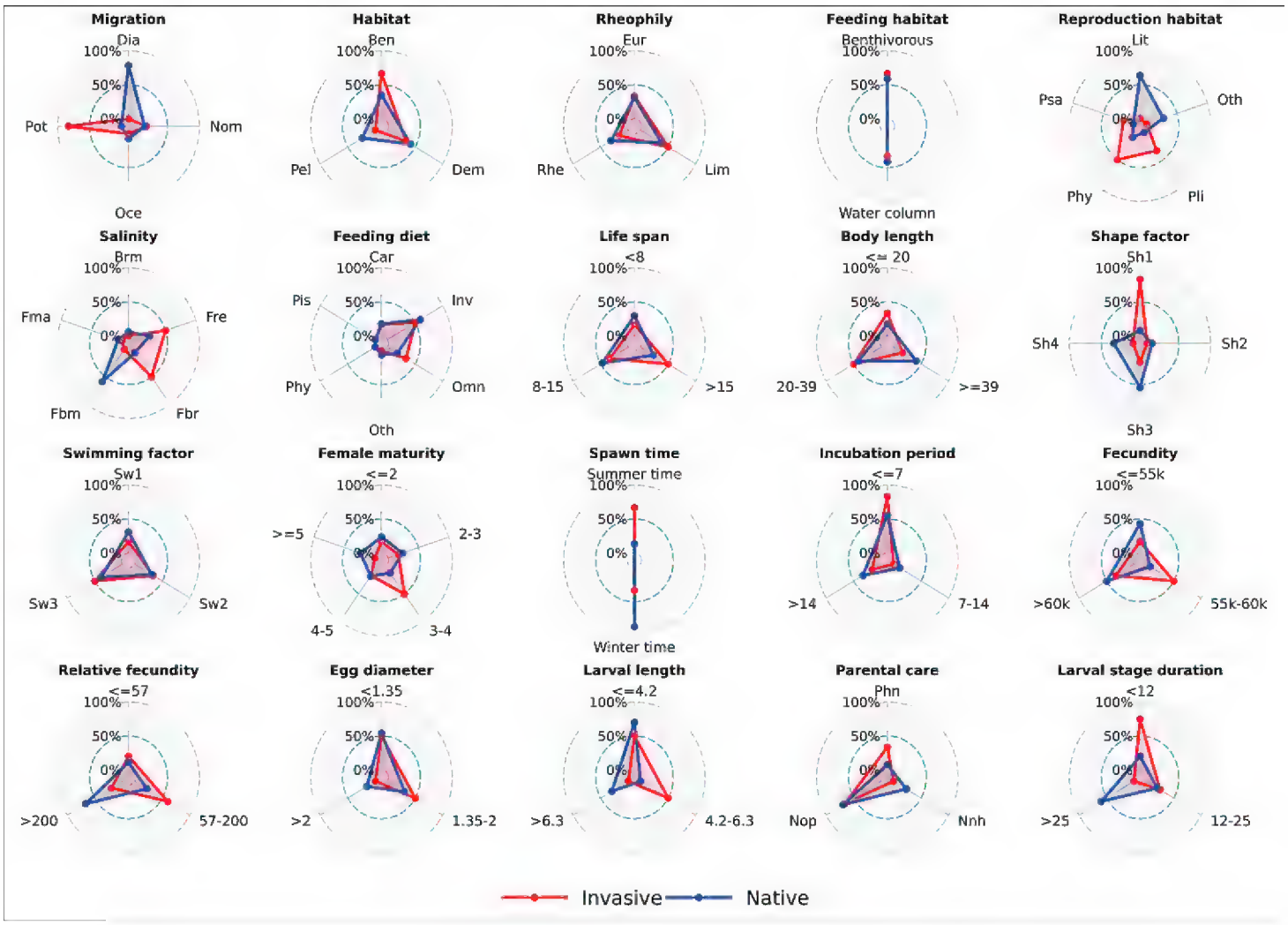



**Figure 3.** Comparison between invasive and native fish species at the Minho Estuary (Portugal) on the average score of each trait modality. The description of all modalities and their units can be found in Appendix 1.

Regarding the strong heatwave events, 31.3% of the traits had a strong decrease during these events (e.g., Egg diameter: >2, decrease of 100%; Habitat: Pelagic, decrease of 100%), and 4.5% had a strong increase (e.g., Migration: Oceanodromous, increase of 291%; Shape factor: 4.35–4.78, increase of 291%) (Table 3).

Over 6% of the traits had a strong decrease in their values during moderate cold-spells' events (e.g., Incubation period: 7–14, decrease of 100%; Salinity: Brackish-marine, decrease of 100%), while about 4.5% of the trait modalities had a strong increase during these extreme events (Migration: Oceanodromous, increase of 450%; Shape factor: 4.35–4.78, increase of 450%) (Table 3).

During the dry events recorded in the Minho Estuary between 2010 and 2019, there was no trait negatively affected by more than >=70.01% of their mean value (Table 3). Only 4.5% of the trait modalities experienced a strong increase in their mean value (e.g., Incubation period: 7–14, increase of 139%; Feeding diet: Other, increase of 139%; Salinity: Brackish-marine, increase of 96%) during dry events (Table 3).

On the other hand, the wet events contributed to strong decreases, 10.4% of the trait modalities were negatively influenced (e.g. Incubation period: 7–14, decrease of 100%; Feeding diet: Other, decrease of 100%) (Table 3). On the other hand, there was no trait positively affected by more than >=70.01% of their mean value during the wet events (Table 3).

**Table 3.** Categorical representation of the influence of the extreme climatic events (temperature heatwaves: moderate and strong, and temperature cold-spells: moderate; precipitation: dry and wet) on the traits modalities of the fish assemblage of the Minho Estuary (Portugal). The traits classification was made considering the traits mean values per event. Classification as: 0 refers to change of ±10% in the traits mean values during the event compared to the mean values during the normal conditions; + refers to an increase in the traits mean values from 10.01 to 40%; ++ refers to an increase in the traits mean values from 40.01 to 70% , +++ refers to an increase in the traits mean values abundance >= 70.01%; - refers to a decrease in the traits mean values from 10.01 to 40%; -- refers to a decrease in the traits mean values from 40.01 to 70% , --- refers to a decrease in the traits mean values >= 70.01%. The description of all modalities can be found in Appendix 1.

| Trait | Modality | Temperature | | | Precipitation | |
|---|---|---|---|---|---|---|
| | | Heatwave | | Cold-spells | Dry | Wet |
| | | Moderate | Strong | Moderate | | |
| Migration | Nom (No migration) | -- | --- | + | - | ++ |
| | Oce (Oceanodromous) | +++ | +++ | +++ | -- | --- |
| | Pot (Potamodromous) | + | ++ | 0 | 0 | + |
| | Dia (Diadromous) | - | --- | - | 0 | - |
| Habitat | Ben (Benthopelagic) | 0 | + | 0 | 0 | 0 |
| | Dem (Demersal) | - | -- | 0 | 0 | 0 |
| | Pel (Pelagic) | ++ | --- | -- | + | --- |
| Rheophily | Lim (Limnophilic) | 0 | + | 0 | 0 | 0 |
| | Eur (Eurytopic) | + | -- | 0 | - | 0 |
| | Rhe (Rheophilic) | 0 | - | - | 0 | 0 |
| Feeding habitat | Benthivorous | 0 | - | 0 | 0 | - |
| | Water column | 0 | + | 0 | 0 | 0 |
| Reproduction habitat | Phy (Phytophilic) | + | -- | - | - | 0 |
| | Lit (Litophilic) | - | - | + | 0 | 0 |
| | Phy (Phyto-litophilic) | + | ++ | 0 | 0 | + |
| | Psa (Psammophilic) | +++ | --- | --- | ++ | --- |
| | Oth (Other) | - | -- | 0 | - | + |
| Salinity | Fre (Freshwater) | 0 | + | 0 | 0 | 0 |
| | Frb (Freshwater-brackish) | ++ | - | + | - | + |
| | Fbm (Freshwater-brackish-marine) | - | --- | - | 0 | - |
| | Fma (Freshwater-marine) | - | --- | 0 | + | --- |
| | Brm (Brackish-marine) | --- | --- | --- | +++ | + |
| Feeding diet | Car (Carnivorous) | - | --- | + | 0 | ++ |
| | Inv (Invertivorous) | + | + | 0 | 0 | 0 |
| | Omn (Omnivorous) | - | 0 | 0 | + | - |
| | Oth (Other) | -- | --- | --- | +++ | --- |
| Life span | <8 | - | - | - | 0 | - |
| | 8–15 | + | ++ | 0 | 0 | 0 |
| | >15 | + | -- | + | 0 | + |
| Body length | <=20 | 0 | + | 0 | 0 | 0 |
| | 20–39 | 0 | -- | 0 | 0 | - |
| | >=39 | + | -- | + | 0 | ++ |
| Body shape | Sh1 (<= 4.35) | + | ++ | + | 0 | + |
| | Sh2 (4.35–4.78) | +++ | +++ | +++ | -- | --- |
| | Sh3 (4.78–5.6) | 0 | --- | -- | 0 | -- |
| | Sh4 (>=5.6) | - | --- | 0 | 0 | + |
| Swimming factor | Sw1 (Fast swimmer) | - | --- | -- | - | -- |
| | Sw2 (Average swimmer) | + | --- | - | - | - |
| | Sw3 (Slow swimmer) | + | ++ | + | 0 | + |

| Trait | Modality | Temperature | | | Precipitation | |
|---|---|---|---|---|---|---|
| | | Heatwave | | Cold-spells | Dry | Wet |
| | | Moderate | Strong | Moderate | | |
| Female maturity | <=2 | - | -- | - | + | - |
| | 2–3 | - | - | + | - | 0 |
| | 3–4 | ++ | - | + | - | + |
| | 4–5 | + | ++ | 0 | 0 | 0 |
| | >=5 | - | -- | + | 0 | ++ |
| Spawn time | Winter time | - | - | 0 | 0 | - |
| | Summer time | + | + | 0 | 0 | + |
| Incubation period | <=7 | + | + | 0 | - | + |
| | 7–14 | -- | --- | --- | +++ | --- |
| | >14 | ++ | --- | -- | + | -- |
| Fecundity | <=55k | - | - | - | 0 | - |
| | 55k–60k | + | ++ | 0 | 0 | + |
| | >60k | + | - | + | - | + |
| Relative fecundity | >=57 | -- | --- | ++ | 0 | + |
| | 57–200 | ++ | - | 0 | - | + |
| | >200 | 0 | --- | - | 0 | - |
| Egg diameter | <1.35 | 0 | + | 0 | 0 | 0 |
| | 1.35–2 | - | --- | 0 | - | 0 |
| | >2 | - | --- | - | + | + |
| Larval length | <=4.2 | 0 | + | 0 | 0 | + |
| | 4.2–6.3 | ++ | - | 0 | - | + |
| | >6.3 | - | --- | - | + | + |
| Parental care | Phn (Protection with nester or eggs hiders) | 0 | ++ | 0 | 0 | + |
| | Nnh (No protection with nester or eggs hiders) | - | --- | - | + | + |
| | Nop (No protection) | + | -- | 0 | 0 | 0 |
| Larval stage duration | <12 | + | - | + | - | + |
| | 12–25 | + | +++ | 0 | 0 | + |
| | >25 | + | - | +++ | + | - |

### Taxonomic composition and functional metrics of the fish assemblage

Over the years, there was a significant reduction in the number of native species, a significant increase in the number of invasive species, and a significant decrease in the taxonomic diversity of the fish community of the Minho Estuary. Significant changes in the functional diversity indices were also recorded for all indices calculated. FDiv, FDis, FEve, FRic, and FRAO decreased significantly through time, while FRed have increased over the years (Fig. 4, Table 4).

## Discussion

We have been monitoring the fish populations in the Minho Estuary for over a decade to better understand the effects of changing environmental conditions on biodiversity. During this period, we have observed signs of decline in both taxonomic and functional diversities, which seems to correspond to a decreasing number of native species and an increasing prevalence of invasive species. This phenomenon seems to be further influenced by changes in environmental factors such as temperature and precipitation,

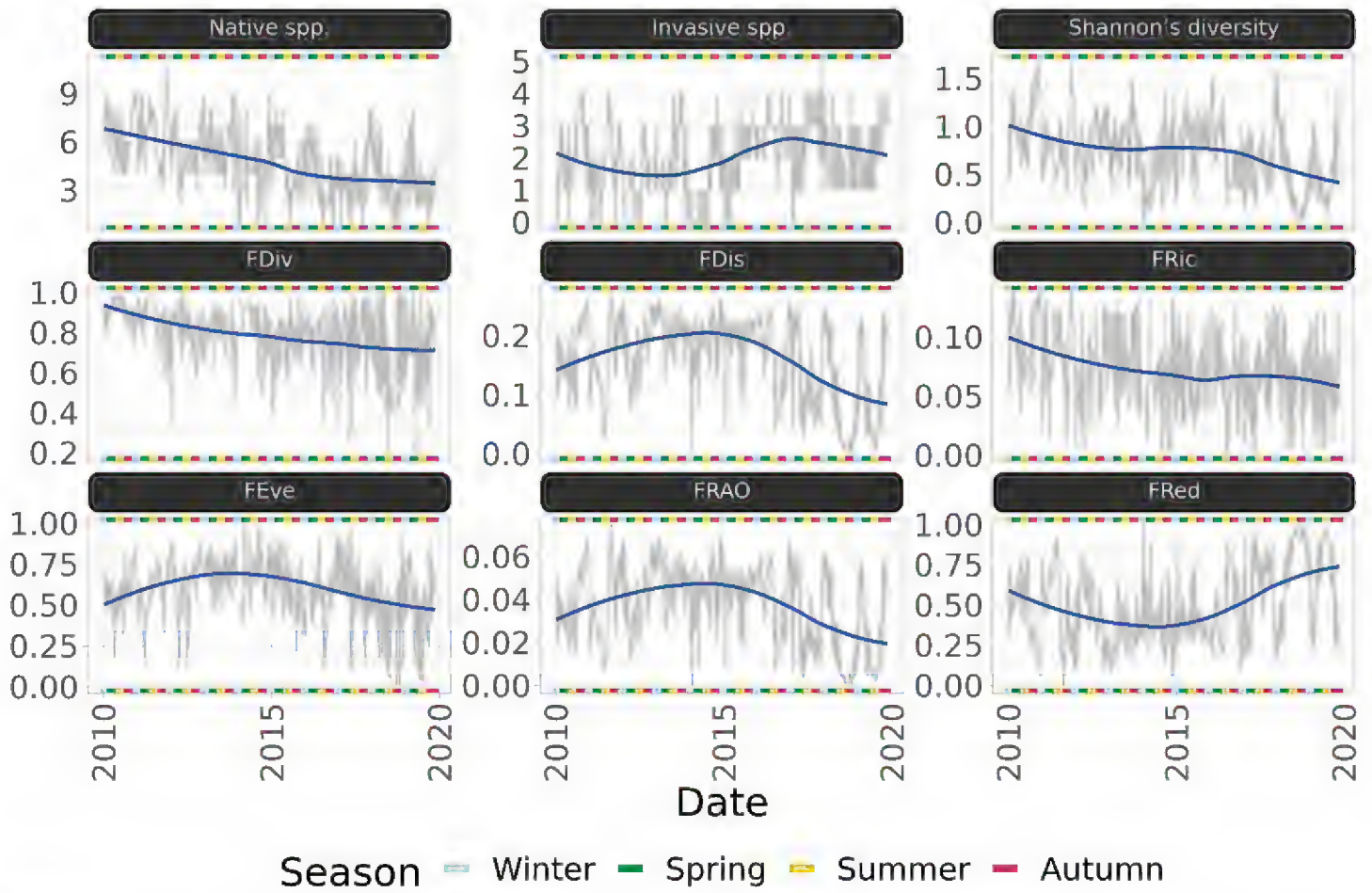



**Figure 4.** Dynamics of the number of native and invasive species, taxonomic diversity (Shannon's diversity) and six functional diversity indices (FDiv, FDis, FRic, FEve, FRAO and FRed) computed with weekly data on the fish captured by fyke nets in Minho Estuary (Portugal) from 2010 and 2019. Blue lines refer to a simple moving regression (loess) and are only indicative of the temporal changes. Statistical tests can be found in Table 4. FDiv = functional divergence, FDis = functional dispersion, FRic = functional richness, FEve = functional evenness, FRAO = Rao's quadratic entropy and FRed = functional redundancy.

which appear to impact several key trait characteristics of these fishes. Overall, there has been a significant shift in fish assemblage occurring in this estuary over the past decade, which now has an almost equal contribution of native and invasive species in terms of species richness, whereas the latter dominate in terms of abundance (Ilarri et al. 2022).

Over the past few years, the Minho Estuary has witnessed a significant increase in populations of invasive species (Sousa et al. 2013; Ilarri et al. 2022). The pumpkinseed, in particular, common carp, and tench are three species that have flourished in the estuary since 2015–2016 (Ilarri et al. 2022), and their increase is likely due to changes in the prevalent environmental conditions. Cano-Barbacil et al. (2022) and Bae et al. (2018) propose temperature as a central factor in explaining the spread of invasive species in the Iberian Peninsula. They emphasize this proposition by pointing out the strong correlation between temperature and thermophilic characteristics of most invasive species, as those from the aforementioned species. Additionally, the pumpkinseed, common carp, and tench prefer slow currents (Benito et al. 2015; Avlijaš et al. 2018; Lages et al. 2021) and highly vegetated zones (Penne and Pierce 2008; Top et al. 2016; Avlijaš et al. 2018), which are likely to become more prevalent with changes in temperature (increase) and rainfall regime (decrease) over time. These three species are also potamodromous, meaning that they perform migrations in the river. In addition,

**Table 4.** Summary of the GAM models with the functional diversity indices calculated with the fish abundances from the Minho Estuary (Portugal) and temperature, precipitation and time. Statistical significance at: $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$. FDiv = functional divergence index, FDis = functional dispersion index, FRic = functional richness index, FEve = functional evenness index, FRAO = Rao's quadratic entropy index, FRed = functional redundancy index, Win = winter, Spr = spring, Sum = summer, and Aut = autumn.

| Index | Temperature | | | | Precipitation | | | | Time | % exp | $r^2$ adj |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | Win | Spr | Sum | Aut | Win | Spr | Sum | Aut | F | | |
| # of native species | 10.32*** | 1.64 | 2.46 | 20.80*** | 3.01* | 2.28 | 6.14* | 1.87 | -11.23*** | 38.8 | 0.374 |
| # of invasive species | 1.02 | 1.65 | 4.24* | 0.70 | 2.76* | 0.89 | 0.04 | 2.16 | 4.44*** | 13.1 | 0.113 |
| Shannon diversity | 2.55 | 0.70 | 0.13 | 0.98 | 2.38* | 0.01 | 1.60 | 0.81 | -4.25*** | 18.0 | 0.170 |
| FDiv | 1.28 | 1.41 | 3.19 | 0.81 | 1.08 | 0.06 | 0.03 | 0.32 | -8.10*** | 16.3 | 0.147 |
| FDis | 2.89* | 0.63 | 0.54 | 0.33 | 5.84*** | 0.67 | 0.70 | 0.00 | -5.08*** | 23.9 | 0.221 |
| FRic | 1.29 | 1.09 | 0.52 | 11.85** | 0.02 | 0.03 | 0.52 | 0.93 | -5.26*** | 11.8 | 0.102 |
| FEve | 2.55 | 1.67 | 0.15 | 6.05* | 0.51 | 1.52 | 3.04 | 0.03 | -3.85*** | 10.8 | 0.093 |
| FRAO | 3.56* | 0.87 | 0.98 | 0.83 | 6.52*** | 0.94 | 0.52 | 0.00 | -4.99*** | 22.5 | 0.206 |
| FRed | 3.96** | 0.14 | 0.48 | 0.68 | 5.65*** | 0.52 | 0.47 | 0.05 | 4.37*** | 20.2 | 0.183 |

they are either phytophilic or phyto-litophilic species, reproducing in areas rich in submerged vegetation and rocks. These species are also either eurytopic (common carp) or limnophilic (pumpkinseed and tench), which means that the common carp tolerates a wide range of environmental conditions, while pumpkinseed and tench are associated with slow moving waters. Interestingly, these three species also have the shape 1 classification in terms of body shape (more rounded and compacted body) and are either average (common carp) or slow swimmers (pumpkinseed and tench) (Schmidt-Kloiber and Hering 2015). The traits' characteristics of these three invasive species seem to have been benefited in the Minho Estuary, as the decrease in precipitation and drought events have contributed to reduced river inflow and water currents in the system. Haubrock et al. (2021) also observed a significant increase over time in short-bodied species with high body depth (shape factor 1) on the Arno River (Italy). According to Vila-Gispert et al. (2005), this trait modality can be advantageous when competing with native species in slow-flow waters. On the other hand, the lower river inflow and water currents are not good for many native species with elongated body shapes that are more associated with fast-flowing waters (rheophilic) and oceanodromous or diadromous migration modalities, such as eel, shad, three-spinned stickleback, European seabass and sea trout. These species have declined sharply over time (Ilarri et al. 2022), and the traits associated with them are also disappearing from the system.

Interestingly, there was a decline in FRic, and an increase in FRed. This suggests that the fish assemblage is losing some traits and that the invasive species are not able to replace the losses of these traits. This is somewhat expected, as invasive species usually differ from native species in their life-history and ecological traits (Vila-Gispert et al. 2005). However, for the vast majority of traits analyzed in the present study, invasive species had very similar modalities to native species, with an important exception of a few traits. One of the most striking differences is probably observed in migration, where the native species have a good amount of diadromous species and almost all

invasive species are potamodromous. This result highlights that climate change is indeed seriously threatening diadromous species (Limburg and Waldman 2009; Mota et al. 2016; Braga et al. 2022; de Eyto et al. 2022), putting additional pressure on this group, which is already heavily impacted (Barbarossa et al. 2020; Duarte et al. 2021; Podda et al. 2022). For diadromous species in the Minho River, in addition to climate change, additional factors such as an increasing number of dams have exacerbated their decline. The work of Azeiteiro et al. (2021) highlights a notable reduction in Allis shad populations due to the increased dam count in the river. The decline of these species is further evident in the significant shift in trait modalities related to salinity preference. In particular, our results show a decline in species that prefer marine and brackish waters, accompanied by a replacement by species that prefer freshwater environments. It is widely reported that climate change may favor marine and brackish water species in this estuary, at least in the near-term (Souza et al. 2018, 2022a). However, this may not be true for all species, as observed in this study. The sampled area is in the upper part of the estuary, where the saline intrusion is historically not so strong, ranging from 0–2.0 psu during late summer month or droughts period (Souza et al. 2013). Despite the decrease in the river inflow and the precipitation regime, it looks like that the saline intrusion is not affecting much the upper estuary, with the exception of European seabass, which in some years can reach the upper parts of the river in summer due to higher saline intrusion (Ilarri et al. 2022). On the contrary, the change in hydrologic conditions seems to favor freshwater species that prefer slow currents or standing waters (limnophilic or eurytopic), which are also invasive (common carp, goldfish, largemouth bass, pumpkinseed, and tench). This might be explained by the decreased hydrodynamics in the area, which started to attract species with affinity to slow moving freshwater.

Another important divergence in trait modality composition between native and invasive species is in the reproduction habitat. Redundancy in this trait is low, with native species preferring to spawn in rocky areas (litophilic species), while invasive species are more associated to densely vegetated areas (phytophilic species) with some rocky bottoms (phyto-litophilic) or in sandy areas (psammophilic species). The decreased rainfall and river inflow probably contributed to the growth of submerged vegetation and the accumulation of finer substrate (sand) in the area. These conditions are also likely behind the invasion success of the aquatic plant *Egeria densa* in the Minho Estuary, which became very abundant after 2015 (authors' personal observation). A change in the phenology of fish species was also observed. Previously, most species had a spawning season associated with the winter season, but with the increase of invasive species in the area, there has been a change in this trait with an increase in the occurrence of species that have a summer spawning season. Fujiwara et al. (2022) also observed an increasing pattern in non-winter spawners and a decreasing trend in winter spawners when analyzing the temporal patterns of estuarine fish communities from the northwestern Gulf of Mexico. Along with the increase in summer spawning species, a reduction in the incubation period (increase in modality less or equal to seven days) was also a feature introduced by the invasive species now present in the area.

Another trait that showed important divergence between native and invasive species is the life span, with native species having a shorter life span than invasive species. This result is interesting as it is largely recognized that successful invasive species have short life spans (e.g. Jaspers et al. 2018), but this may be different for freshwater fish species in the Iberian Peninsula (e. g. Vila-Gispert et al. 2005). In this region, many of the invasive aquatic organisms arrived several centuries ago and were influenced in the past by the wishes of the rulers of society (monarchs), who deliberately introduced species from Central Europe (Clavero 2022). This important remark is necessary because the characteristics of the traits of the invasive species currently found in the studied system may not be initially selected by the environment, but by men attempting to create an ecosystem similar to that observed in Central Europe. Of the invasive fish species recorded in our study, two originate from North America (largemouth bass and pumpkinseed), while the common carp, goldfish, and tench originate from Eurasia, and the Iberian gudgeon is native to other areas of the Iberian Peninsula but not to the Minho Estuary. Another noteworthy aspect regarding invasive species in the Minho Estuary is that a significant proportion of them consists of species targeted by recreational fisheries, which, usually have different traits when compared with their native counterparts. The introduction of these species follows a meticulous selection by humans aimed at propagating certain desirable traits for angling activities, notably larger body size and a wide ecological tolerance (Alcaraz et al. 2005; Grabowska and Przybylski 2015). Unfortunately, the illegal introduction of species targeted by recreational fishermen in the Iberian Peninsula is still a problem (Clavero and Hermoso 2011).

The traits of fish species are influenced by environmental conditions and are therefore good predictors of how fish species will respond to different climate change events (Winemiller and Rose 1992; Dahlke et al. 2020). The effects of extreme weather events on fish species varies from species to species, probably related to the sensitivity of each species to the type and intensity of the event. Overall, extreme weather events had mostly strong negative effects on fish traits modalities than positive ones (i.e. decreases on the values of trait modalities were more frequent than increases). In our study, heatwaves had the greatest impact on traits compared to the other extreme events. Indeed, Barbarossa et al. (2021) suggest that increases in water temperature constitute a larger threat to freshwater fishes than changes in high and low flow conditions. The heatwaves caused a decline in trait modalities associated with higher salinity preference, reproduction in sandy habitats (Psammophilic), longer body (species with higher shape factors), average and fast swimmers, longer incubation period, low fecundity, high egg diameter, and longer larval length. On the other hand, it was observed a total benefit for short-bodied species. Our results are in part corroborated by Fujiwara et al. (2022), that suggested that fish species sensitive to changes in temperature, generally have traits associated with longer generation time, maximum length and length at maturity. In our study, traits associated with these aspects negatively responded to extreme temperature events. Interestingly, these trait modalities were also negatively correlated with the long-term effects of temperature. Therefore, the heatwave events (especially the strong ones) are possibly accelerating the speed of change in the fish community in Minho Estuary.

Regarding extreme precipitation weather events, both dry and wet events can be critical in estuarine ecosystems due to the hydrological dynamics of these systems. Although the extreme dry events correlated with a large number of species (Ilarri et al. 2022), these events seem to have a broad effect on the whole fish community, with fish traits benefiting more than being negatively affected (mainly considering cases where there was a change in abundance ≥ 70.01%). This result differs from our expectations, as we expected that these conditions have mainly negative impacts on the fish functional diversity. Normally, extreme dry events are associated with an increase in salinity and changes in other water biochemical properties (Martinho et al. 2007; Kinard et al. 2021). In this case, salinity and water quality act as abiotic filters in the fish assemblage and select fishes with traits better adapted to harsh conditions (Kinard et al. 2021). Overall, drought events were linked to an increase in the abundance of trait modalities associated with the marine environment (brackish-marine), which was expected as the decreasing water flow can lead to stronger saltwater intrusion into the upper parts of the estuary. Drought events also positively correlated with some traits modalities related to reproduction, such as incubation period, egg diameter and larval length. The favored modalities are not in the extremes of the ranges of the traits, suggesting that they might be indicative of moderate and stable environments, which also suggested that drought events probably did not cause severe stress to the fishes in Minho Estuary. On the other hand, the extreme wet events, despite of affecting a lower number of species than the extreme dry events (see Ilarri et al. 2022), they affect negatively several trait modalities. This result was also different than expected, as areas with more precipitation are normally expected to create more stable conditions than areas submitted to dry conditions. In this sense, wet events can be expected to affect the extreme modalities of traits, and to favor the moderate modalities of traits, which was not the case for several traits in this study. The extreme wet events were mostly linked to a decline in traits associated with the marine environment, such as oceanodromous and freshwater-marine modalities, which makes sense given the lower saline influence under this condition. Other traits' modalities that were negatively correlated were pelagic, psammophilic, shape 2 and incubation period of 7–14 (intermediary modality).

Some studies indicate that changes in functional diversity are easier to detect than changes in taxonomic diversity and serve as early warning signals for threatened ecosystems. However, in this study it was possible to see the same signal in both metrics, suggesting that in the Minho Estuary the deterioration of taxonomic and functional diversity occurred simultaneously. Each functional diversity index provided a different perspective on the functional change that is occurring in the system. For example, the decrease in the FDiv index indicates that some of the most abundant species in the system nowadays have highly convergent characteristics, while FDis, FRic and FRAO tell more or less the same story, namely that the fish assemblage is losing trait richness and diversity, and particularly rapidly after 2015, a period when the dominance of a few invasive species increased significantly. The FRed index, which is a potential early warning indicator of increasing disturbances in the system (van der Linden et al. 2016), shows that the fish assemblage is becoming more functionally redundant. This

result may indicate two different things: first, that some traits that were present, but not dominant are being lost; and second, that the remaining traits are more similar to each other, which may provide some resilience to the assemblage in terms of functional stability (van der Linden et al. 2016).

## Conclusion

The findings of this study demonstrate the negative impacts of climate change and extreme weather on fish communities in estuarine ecosystems. The decline in both taxonomic and functional diversity suggests a threat to the overall balance and health of the ecosystem. These changes show no signs of slowing down, highlighting the need for immediate and effective action to mitigate environmental damage caused by climate change. Furthermore, this loss in fish diversity has implications for local cultures and economies that rely on fish as a source of food and income. It is therefore crucial to address climate change before further harm is inflicted on fish communities and the humans they support.

## Author contributions statement

Conceptualization: ATS, MI. Data curation: ATS, MI. Formal analysis: ATS, MI. Investigation: ATS, CA, ED, MI. Methodology: ATS, CA, MI. Project administration: CA. Resources: CA. Software: ATS, MI. Validation: ATS, CA, ED, MI. Visualization: ATS, MI. Writing original draft: ATS, MI. Writing, review and editing: CA, ED.

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## Appendix 1

**Table A1.** Fish traits and modalities descriptions based on the information contained in the www.freshwaterecology.info database.

| Trait category | Trait | Trait abbreviation | Modality | Modality description |
|---|---|---|---|---|
| Biological | Body length | bod | bl1 | Smaller or equal to 20 cm |
| | | | bl2 | Between 20 and 39 cm |
| | | | bl3 | Larger or equal to 39 cm |
| Biological | Egg diameter | egg | ed1 | Smaller than 1.35 mm |
| | | | ed2 | Between 1.35 and 2 mm |
| | | | ed3 | Larger than 2 mm |
| Biological | Fecundity (# of oocites) | fec | fe1 | Less or equal to 55000 |
| | | | fe2 | Between 55000 and 60000 |
| | | | fe3 | More than 60000 |
| Biological | Feeding diet | die | car | Carnivorous |
| | | | inv | Invertivorous |
| | | | omn | Omnivorous |
| | | | oth | Other |
| | | | pis | Piscivorous |
| | | | phy | Phytophagous |
| Biological | Female maturity | fem | ma1 | Before 2 years |
| | | | ma2 | Between 2 and 3 years |
| | | | ma3 | Between 3 and 4 years |
| | | | ma4 | Between 4 and 5 years |
| | | | ma5 | After 5 years |
| Biological | Incubation period | inc | ip1 | Less or equal to 7 days |
| | | | ip2 | Between 7 and 14 days |
| | | | ip3 | More than 14 days |
| Biological | Larval length | lar | ll1 | Smaller or equal to 4.2 cm |
| | | | ll2 | Between 4.2 and 6.3 cm |
| | | | ll3 | Larger than 6.3 cm |
| Biological | Duration of larval stage | ldu | ld1 | Less than 12 days |
| | | | ld2 | Between 12 and 25 days |
| | | | ld3 | More than 25 days |

| Trait category | Trait | Trait abbreviation | Modality | Modality description |
|---|---|---|---|---|
| Biological | Life span | lif | ls1 | Less than 8 years |
| | | | ls2 | Between 8 and 15 years |
| | | | ls3 | More than 15 years |
| Biological | Parental care | par | nnh | No protection with nester or egg hiders |
| | | | nop | No protection |
| | | | pnh | Protection with nester or egg hiders |
| Biological | Relative fecundity[1] | rel | fr1 | Less or equal to 57 |
| | | | fr2 | Between 57 and 200 |
| | | | fr3 | More than 200 |
| Biological | Shape factor[2] | sha | sh1 | Ratio smaller or equal to 4.35 |
| | | | sh2 | Ratio between 4.35 and 4.78 |
| | | | sh3 | Ratio between 4.78 and 5.6 |
| | | | sh4 | Ratio larger than 5.6 |
| Biological | Spawn time | spa | st1 | Winter time |
| | | | st2 | Summer time |
| Biological | Swimming factor | swi | sw1 | Fast swimmer |
| | | | sw2 | Average swimmer |
| | | | sw3 | Slow swimmer |
| Ecological | Feeding habitat | fee | ben | Benthivorous |
| | | | wat | Water column |
| Ecological | Habitat | hab | ben | Benthopelagic |
| | | | dem | Demersal |
| | | | pel | Pelagic |
| Ecological | Migration | mig | dia | Diadromous |
| | | | nom | No migration |
| | | | oce | Oceanodromous |
| | | | pot | Potamodromous |
| Ecological | Reproduction habitat | rep | lit | Lithophilic |
| | | | oth | Other |
| | | | phy | Phytophilic |
| | | | pli | Phyto-litophilic |
| | | | psa | Psammophilic |
| Ecological | Rheophily | rhe | eur | Eurytopic |
| | | | lim | Limnophilic |
| | | | rhe | Rheophilic |
| Ecological | Salinity | sal | brm | Brackish-marine |
| | | | fbm | Freshwater-brackish-marine |
| | | | fbr | Freshwater-brackish |
| | | | fma | Freshwater-marine |
| | | | fre | Freshwater |

[1]Maximum number of oocites per 100g [2]Total length divided by maximum body depth.

# Appendix 2

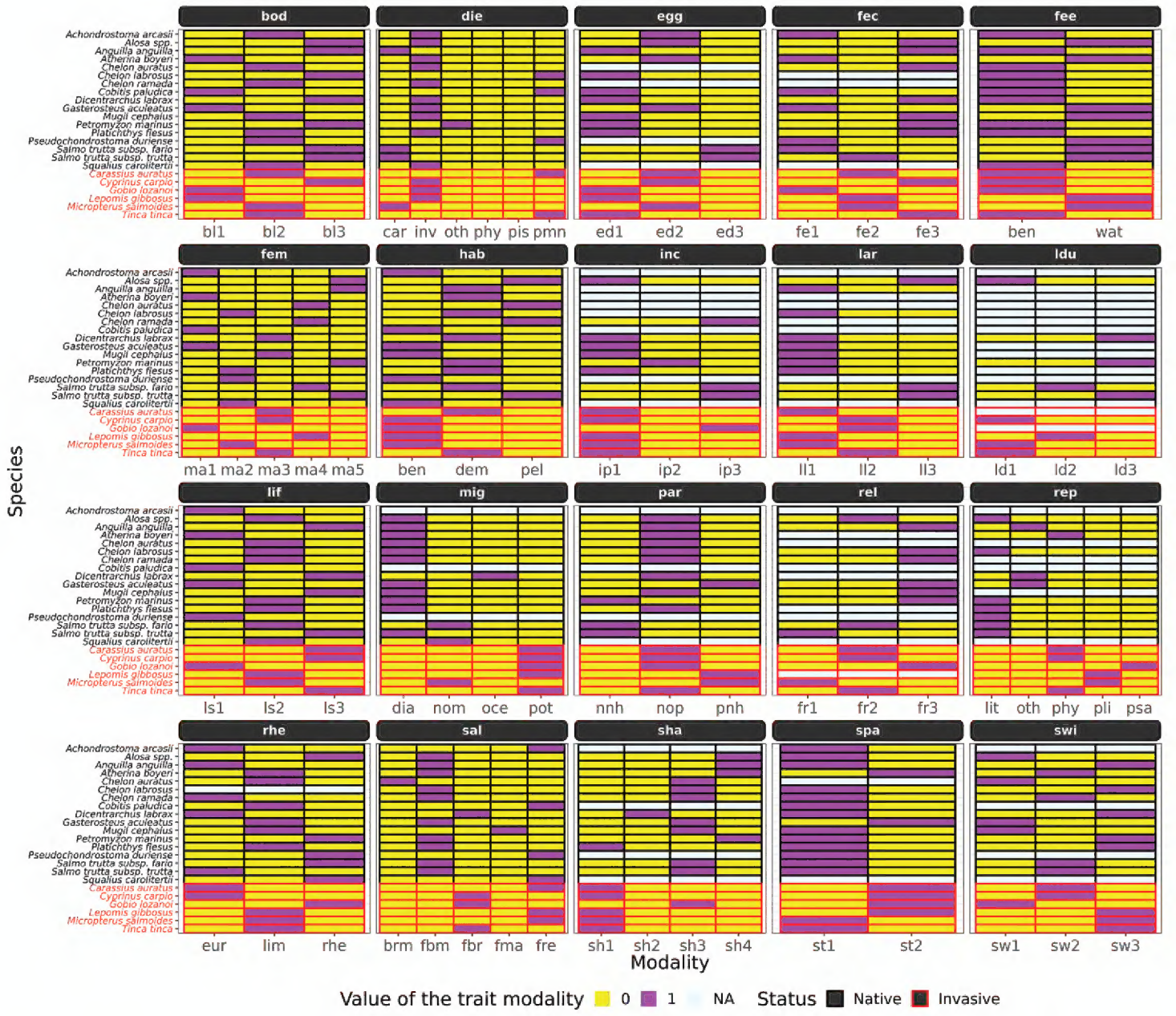


**Figure A1.** Values of the modalities of each trait from the fish species captured in the Minho Estuary by fyke nets throughout the course of a decade (2010–2019). Modality classification was based on the information contained in www.freshwaterecology.info database and complemented by the information present on Cano-Barbacil et al. (2020). For the description of traits and modalities see Appendix 1.

## Supplementary material 1

**Daily air temperature and precipitation data, extracted from the NASA Langley Research Center (LaRC) POWER Project website**

Authors: Allan T. Souza, Ester Dias, Carlos Antunes, Martina Ilarri

Data type: csv

Explanation note: The data ranges from 2010-01-01 to 2019-12-31 (yyyy-mm-dd).

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Link: https://doi.org/10.3897/neobiota.88.108283.suppl1